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Biological soil crusts in a northeastern pine barren: Composition and ecological effects

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Abstract

Biological soil crusts (BSCs), otherwise known as cryptogamic soil crusts, biocrusts, or cyanobacterial crusts, are soil aggregations hosting diverse biotic communities. They are composed of cyanobacteria and algae, and generally have a covering of moss and/or lichen. BSCs are typically found in arid to semi-arid regions throughout the world, and are integral soil stabilizers, moisture retainers, and nitrogen fixers in these communities. Along with these factors, BSCs are able to impact germination and establishment of plants, either as an accompanying influence, or direct result of those listed above. BSCs have yet to be formally described in the inland northeastern United States, and yet they have been found in a variety of locations, including New York, New Hampshire, and Maine. This paper seeks to investigate the species composition of crusts and their effects on seedling germination in the Albany Pine Bush Preserve, an inland scrub-oak pine barren ecosystem in upstate New York. Crusted and non-crusted soil samples were taken from the Preserve and refrigerated at 4°C until use. Several of the crusted samples were sent off for analysis of their constituents, and the other eighty dishes (forty crust and forty sand) were used in the germination experiment. Three species of plants native to the Pine Bush (little bluestem (*Schizachyrium scoparium*), bush clover (*Lespedeza capitata*), and lupine (*Lupinus perennis*)) were scattered onto the soil conditions, with twenty seeds of one species in each dish. The results of this study supported our hypothesis that BSCs would inhibit the success of seedling germination, with bush clover and lupine germinating three and five times greater, respectively, on bare sand than crusted conditions. The crusts' ability to influence the presence of plant species suggests a larger impact on the whole ecosystem, as those that succeed will affect other present biota. Crusts likely contribute to habitat heterogeneity, given their apparent influence on seeds and the crusts' spatial variation throughout the environment. Further research into the impact of crusts in

northeastern systems should be undertaken, as crusts' impacts are significant and may be different than those described in arid and semi-arid systems.

Introduction

Biological soil crusts (BSCs) are soil aggregations of bacteria, algae, lichens, and bryophytes that form thin layers on soil surfaces. They can play an integral role in soil stability (Aguilar et al. 2009, Belnap & Gillette 1997), soil moisture retention (Asplund & Wardle 2017, Bu et al. 2015), and chemical processes such as nitrogen and carbon fixation (Belnap 2002, Billings et al. 2003, Castillo-Monroy et al. 2010). BSCs have been most-often studied in arid to semi-arid ecosystems, where they can make up a large portion of the ground biota. They are found not just in these locations, however, as they also occur in temperate areas where there is reduced plant cover (Belnap 2003). Despite this, minimal study has been done in the northeastern United States, and what has been published on the topic mostly focuses on the recognition and ecology of crusts in coastal plain and dune ecosystems (e.g. Sedia and Ehrenfeld 2003, Smith et al. 2004, Thiet et al. 2014). BSCs have also been reported as existing in inland pine barren ecosystems, like that of New York and New Hampshire, and yet no formal recognition has been made. It is because of this that we seek to investigate the components and ecological processes of crusts in the Albany Pine Bush Preserve.

Much research has gone into the investigation of how BSCs affect the germination and establishment of plants (Serpe et al. 2008, Su et al. 2009, Zaady et al. 1997). Many of these interactions are based on mechanical factors. Some authors state that the physical nature of the crust can impact germination, as some plants may not have the capabilities to penetrate the surface with their roots. Even the crusts' physical morphology influences how materials, including seeds, move across its surface (Belnap 2003). Seeds have the potential to be blown off of smooth crusts, and yet BSCs with cracks or ridges may be able to provide seeds with areas of extra moisture that the crust would have otherwise absorbed, that is if the seed manages to fall in via wind, water, or animal influence (Belnap et al. 1999). It can also come down to the physical properties and needs of the species of plant trying to germinate, as some with different nutrient requirements or succession types are able to withstand the crust's micro-environment better than others.

Chemical properties of the crust and its constituents also influence the ability of a seed to germinate and establish successfully. Crusts are able to alter available nutrients (Belnap 2003), and certain BSCs have been documented as having a slightly alkaline pH (Liu et al. 2017, Abed et al. 2013). This change in pH from the soil's average thus impacts the availability of nutrients that are accessible to, and potentially needed by, the vascular plant community (Belnap and Lange 2017). The ability of crustal organisms to fix nitrogen and provide a carbon resource would make them a facilitating factor for plants, though there has been documentation of plant/crust competition for nutrient resources (Harper & Belnap 2001). Overall, the results detailed in the literature are mixed, with crusts having positive (Hawkes 2004, Pendleton et al. 2003), negative (Langhans et al. 2009 [A], Serpe et al. 2006), or mixed effects (Deines et al. 2007, Harper and Belnap 2001, Anderson et al. 1982) on the success of seedlings being able to germinate. Moreover, each experiment's results tend to be specific to which species of plants and crustal organisms were used/present.

This study seeks to document the composition of the crusts at the Albany Pine Bush Preserve in upstate New York, USA, and assess their ecological influence on plant seedling germination. Germination is an important stage of plant establishment, and so any filtering that crusts do may affect both the composition and spatial heterogeneity of the plant community.

This is the first known examination of BSCs at this location, and adds needed understanding to the ecology of crusts in the temperate northeast.

Materials and Methods

The Albany Pine Bush Preserve is an inland sand plain that is a product of deep sandy glacial outwash soils. Though its climate is cold temperate that supports nearby eastern deciduous forest, its vegetation is open due to the edaphically xeric conditions and frequent fires. Native vegetation is dominated by scrub oak (*Quercus ilicifolia*) and scattered pitch pine (*Pinus rigida)*. Areas of the Preserve were invaded by the non-native black locust tree (*Robinia pseudoacacia*) in the latter 20th Century and subsequently restored with mechanical removal of locust stems and roots (Rice et al. 2004).

Sample collection

In order to document the species composition of moss, lichen, and algae within the Albany Pine Bush Preserve, samples of BSCs were collected from 12 management units of the Preserve, including native pitch pine barren habitat and restored successional sandplain habitat. The purpose of the sampling was to capture the range of moss and lichen species present at the Preserve. Mosses were described to species by Lorinda Leonardi of the New York State Museum. Specimens have been catalogued in their permanent collection for future reference. Lichens were described to species by Dr. Rachel Thiet of Antioch College.

We collected crust samples for our germination experiment from a single site that had been cleared of the black locust tree in 2008 and subsequently replanted with a native species mix including little bluestem (*Schizachyrium scoparium*), wild lupine (*Lupinus perennis*) and bush clover (*Lespedeza capitata*). We inserted 40 3.5cm plastic petri dishes into the soil to collect mature moss-dominated crusts in the dish. Crusts were dominated by two moss species, *Ceratodon purpureus* and *Polytrichum commune.* Lichens made up a minor component, though several moss-crust dishes started developing lichens once watering began We also collected 40 dishes of bare sand with no visible moss or lichen, though some dishes turned green from developing algal mats during the experiment, indicating that algae and cyanobacteria were likely present. All dishes were covered, taken back to the lab, and stored in a refrigerator at 4°C until the beginning of the experiment.

Germination Procedure

Locally field-collected seeds of little bluestem, bush clover, and lupine were graciously given to us from the staff at the Albany Pine Bush Preserve. There were two soil conditions in this experiment: moss-crust and sand. 20 seeds per dish of a single species were scattered onto the surface; seeds were not buried so as to best mimic natural wind-dispersal. There were ten replicate dishes for each species-soil condition combination, with 60 dishes total. Finally, 20 additional dishes were established as a control for seeds emerging from a potential buried seed bank; no seeds were added to this latter treatment.

Dishes were laid out randomly on a light table under 12-hour white light, and were rotated once a week to eliminate discrepancies in light conditions. All dishes were watered with 5ml of water every day. All dishes were checked for apparent germination every 1-2 days for 35 days. Seeds were considered to have germinated at emergence of the radicle, and were subsequently removed.

Data Analysis

We used two-way ANOVA (R version 3.4.1) to analyze the effect of soil type (moss-crust versus sand) and species on the total number of seeds that germinated. Little bluestem germination was extremely low in both conditions, and so was omitted from data analysis.

Results

Composition of crust communities

Table 1) Moss and lichen species identified in Albany Pine Bush biological soil crusts.

Scientific name	**Common name**
Mosses	
Ceratodon purpureus (Hedw.) Brid.	Fire Moss
Polytrichum commune Hedw.	Common Haircap
Lichens	
Cladonia gracilis ssp. turbinada	Smooth Cladonia
Cladonia ochrochlora	Smooth-footed Powderhorn
Cladonia verticillata	Ladder Lichen
Cladonia chlorophaea	Mealy Pixie Cup

Mature crusts were visible throughout the Albany Pine Bush Preserve, scattered among vascular plants in areas with low canopy coverage. Mosses were more abundant, with lichens being only occasionally observed. Soil consolidation ranged from incipient algal crusts to solidly consolidated moss-crusts. Four lichen species, all of the genus *Cladonia,* and two species of mosses were identified (Table 1). Even in areas of open sand, green hues were visible on the top, indicating the development of algal mats.

Germination Success

No seeds germinated in either our moss-crust nor sand control dishes, and so a seed bank did not appear to be present.

Overall, germinating seeds ranged from 0 to 8 out of 20 per dish in the crust condition, and 0 to 14 out of 20 per dish in the bare sand condition. Some seeds also turned black and did not germinate. It is possible that this was a result of over-watering, and thus caused decay. On the uncrusted conditions, bush clover had a greater initial rate of germination compared to lupine. By the 17th day, bush clover's germination rate dropped substantially, while lupine's continued to rise (Figure 2). By the 35^{th} day of the experiment, the cumulative germination totals of each species were similar (Table 2; Figure 1).

Three and five times more bush clover and lupine, respectively, germinated on bare soil than crusted dishes (Table 2; Figure 1). There was no interaction between soil type and plant species on germination.

Discussion

This study offers the first description of biological soil crusts in the inland northeast. Thus far, studies of BSCs in this area has been limited, not because of a lack of crusts present, but a lack of scientists investigating these dynamic soil aggregates (Belnap and Lange 2001). There has been an increased awareness of their presence in the northeast, however, and several studies have begun to document them and their properties. New Jersey (Sedia and Ehrenfeld 2003) and Cape Cod (Smith et al. 2004, Thiet et al 2014) have been the starting points for this research, and more is being done. Corbin and Thiet (in prep) established that crusts are widespread in glacial remnant barren ecosystems within the northeast including New York, New Hampshire, Massachusetts, Vermont, and Maine. The Albany Pine Bush fits squarely into that broader regional ecosystem.

Our experimental test clearly showed that moss-covered BSCs at the Albany Pine Bush inhibit the germination of both species of plants. Germination rate as well as the total amount was similar between the two natives, so the effects do not appear to be species-specific. Several other studies have also found negative effects of crusts on seed (Jeschke and Kiehl 2008, Serpe et al. 2006), but other sources have found positive, mixed, and/or species-specific effects. From the collective literature, it is once again important to realize the array of effects BSCs can have on the dynamics of an ecosystem, including plant germination and establishment.

Several mechanisms have been offered to explain crusts' inhibition of germination. One is that water is more limiting to seeds on crusts. Despite the fact that crusts are able to provide essential nutrients to developing embryos, bare soil provides seeds with a larger area of contact and potentially more moisture (Song et al. 2017). During our experiment, the bare soil would often cover up seeds as a result of the watering process, providing the extra soil contact that Song et al. described. Soil moisture is often a limiting factor for plants, and as such, germination and establishment success is positively correlated with the amount of water present (Li et al. 2005). Moss-dominated crusts, as were present in this experiment, appeared to quickly absorb the moisture provided, preventing the seeds from imbibing water unless they managed to fall beneath the canopy where there was less potential evaporation. Comparatively, the bare soil conditions had no means of water drainage, leaving only the seeds present in the dish to absorb the water. Hawkes (2004) found that a high-water treatment caused a higher germination rate. This ability for bare soil to provide more moisture may even override the potential benefits the crusts could provide (Li et al. 2005), meaning more seeds germinating on bare soil.

Mechanical inhibition has been another heavily documented result in the literature. Crusts, with their layers of lichen and moss and ability to hold soil particles tightly together, create a very hard surface for vascular plants to establish on. Deines et al. (2007) showed that there was a significant inability of the species tested to penetrate lichen-covered BSCs as compared to bare soil. It stands to reason that if a seed does not have the correct drilling mechanism to penetrate the earth, it will not be able to grow in that location. Boeken et al. (2004) found that their species of study (*Stipa capensis*) was able to germinate much more successfully on BSCs, and this could have been a result of their boring mechanism in dense crust-covered areas. Langhans et al. (2009) [A] demonstrated that germinated seeds appeared in the cracks of the crust, bypassing the possibility of mechanical inhibition. This appeared to be the same in our study, with most seeds that managed to germinate on the crusts being found beneath the crust canopy. It is worth noting that we tallied germination without waiting for roots to penetrate the soil and establish; as a result the negative effects of crusts on germination that we observed may be conservative.

Finally, crusts have the potential to inhibit germination by chemical means. Though crusts may provide plants on and around them with usable nitrogen and carbon (Belnap and Lange 2017, Harper and Belnap 2001) as well as other essential nutrients (Zhang et al. 2016), the literature also points out that allelopathic influences could be at work. Lichens growing on acidic soils have been documented as having secondary allelopathic effects on plants and animals. Their ability to release lichen acids can have an inhibitory effect on germination (Sedia and Ehrenfeld 2003). It is noted by Gardner and Mueller (1981) that those lichens growing on alkaline soils typically do not produce these secondary compounds, and because crusts have been shown to be more alkaline in desert ecosystems (Liu et al. 2017), it is possible that they are not affecting germination through these means. However, because we did not test our soil pH, it cannot be ruled out as a possibility, as crusts in temperate regions may have a differing effect on soil pH.

Though the literature has often shown species-specific differences contributing to the data of their results, both species we analyzed responded similarly. Bush clover had a greater initial germination rate than lupine on the bare soil condition, though the difference between the species by the end of the experiment was not significant. Bush clover seeds are smaller, so they could imbibe water more quickly, and also may be able to fall in between the cracks and have access to more moisture than the larger lupine seeds. Meanwhile, big seeds are able to remain on top of the crust and have prime access to sunlight (Serpe et al. 2006). Still, there was no significant difference between the abilities of bush clover and lupine to germinate. This is interesting to note, as many studies have found that different species have different success at germinating on crusts. Godinez-Alvarez et al. (2012) found that all three species of vascular plants studied had different responses to different types of BSCs, with cyanobacterial crusts positively affecting *A. marmorata* and *N. tetetzo*, and negatively affecting *P. laevigata*. Other studies have had similar results (Hawkes 2004, Bliss and Gold 1999) and so it is likely that expanded research into various other species in the Pine Bush could show these multifarious effects.

The crusts at the Albany Pine Bush Preserve not only survive frequent fires, but may also be dependent on them to maintain an open canopy. O'Bryan et al. (2009) found that disturbance by fire increased both the species diversity and abundance of crusts, likely due to the increased availability of light in these plots. The fires are also likely to influence the species composition of the BSCs. Bowker et al. (2004) found that low-intensity wildfires had little apparent effect on the condition of BSCs, though they did describe a shift in the species composition with relation to fires. Crusts have been documented as having a slow recovery process with regards to trampling (Cole 1990, Barger et al. 2006), as well as intense fires (Kasper 1994, Johansen 2003). Some even cite a dramatic reduction in the presence of lichen, algae, and cyanobacteria in burned plots (Johansen et al. 1984). However, the prescribed fires conducted at the Albany Pine Bush do not seem to fall into this high-disturbance category. The Albany Pine Bush had a greater proportion of moss-dominated crusts than other northeastern barrens where fire was infrequent (Corbin and Thiet, *manuscript in prep*), and in particular we note the importance of fire moss at our site, which is tolerant of fires and may be able to start the succession pattern, allowing crusts to re-establish (Clément and Touffet 1990). Nearly all of our understanding of BSCs' response to fire comes from dryland ecosystems, however, and so further research is needed to understand the dynamics in this wetter climate. Johansen et al. (1984) noted that at their study site in Utah, algae were able to have a rapid recovery time, perhaps as a result of unusually rainy years following the initial burn. Langhans et al. (2009) [B] found consistent results in temperate Germany, with algae numbers high in initial crusts, and decreasing with increasing crust age. With the Albany Pine Bush being in a temperate area with a greater average annual rainfall than Utah, this may accelerate the healing process of crusts in response to any damage done by fire.

By significantly inhibiting the germination of both lupine and bush clover, BSCs appear to influence the ecology of the Pine Bush Preserve by impacting which plants are able to succeed in germinating. Their ability to influence the spatial patterning of vascular plants would overall increase habitat heterogeneity for the ecosystem (Kidron and Aloni 2017). Given that the literature shows, more often than not, that different species respond with different success rates for both germination and establishment, this seems to support the idea of a heterogeneous system.

We emphasize that crusts remain an under-appreciated component of northeastern ecosystems, and that they may play a larger role here than previously recognized. More research is already in the process, with sampling of crusts in the northeast being done by

Corbin and Thiet (in prep). Ultimately, more study must be done on these temperate-region crusts. The differences between those in the well-documented arid and semi-arid regions could be great, and their needs and impacts could be as well.

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Citations

Abed, R.M.M., Al-Sadi, A.M., Al-Shehi, M., Al-Hinai, S., Robinson, M.D. “Diversity of free-living and lichenized fungal communities in biological soil crusts of the Sultanate of Oman and their role in improving soil properties”. *Soil Biology & Biochemistry*, Vol. 57, 2013, pp. 695-705.

Aguilar, A.J., Huber-Sannwald, E., Belnap, J., Smart, D.R., Moreno, J.T.A. “Biological soil crusts exhibit a dynamic response to seasonal rain and release from grazing with implications for soil stability”. *Journal of Arid Environments*, Vol. 73, No. 12, 2009, pp. 1158-1169.

Anderson, D.C., Harper, K.T. and Holmgren, R.C. “Factors influencing development of cryptogamic soil crusts in Utah desert. *Journal of Range Management*, Vol. 35, No. 2, 1982, pp. 180-185.

Asplund, Johan and Wardle, David A. “How lichens impact on terrestrial community and ecosystem properties”. *Biological Reviews*, Vol. 92, 2017, pp. 1720-1738.

Barger, N.N., Herrick, J.E., van Zee, J., Belnap, J. “Impacts of biological soil crust disturbance and composition on C and N loss from water erosion”. *Biogeochemistry*, Vol. 77, No.2, 2006, pp. 247-263.

Belnap, J. “Nitrogen fixation in biological soil crusts from southeast Utah, USA”. *Biology and Fertility of Soils*, Vol. 35, No. 2, 2002, pp. 128-135.

Belnap, J. “The world at your feet: desert biological soil crusts”. *Frontiers in Ecology and the Environment*, Vol. 1, No. 4, 2003, pp. 181-189.

Belnap, J., Williams, J., and Kaltenecker, J. “Structure and function of biological soil crusts”. *Proceedings: Pacific Northwest Forest and Rangeland Soil Organism Symposium*, Vol. 461, USDA Forest Service General Technical Report Pacific Northwest, 1999, pp. 161-178.

Belnap, J. and Gillette, D.A. “Disturbance of biological soil crusts: Impacts on potential wind erodibility of sandy desert soils in southeastern Utah”. *Land Degradation & Development*, Vol. 8, No. 4, 1997, pp. 355-362.

Belnap, J. and Lange, O.L. “Belnap and Lange: Chapter 10: Lichens and Microfungi in Biological Soil Crusts: Structure and Function Now and in the Future”. *The fungal community: its organization and role in the ecosystem*, 2017, pp. 137-157.

Belnap, J. and Lange, O.L. “Belnap and Lange (eds.) Biological Soil Crusts: Structure, Function, and Management”. *Ecological Studies*, Vol. 150, 2001, pp. 1-30.

Billings, S.A., Schaeffer, S.M., Evans, R.D. “Nitrogen fixation by biological soil crusts and heterotrophic bacteria in an intact Mojave Desert ecosystem with elevated CO2 and added soil carbon”. *Soil Biology & Biochemistry*, Vol. 35, No. 5, 2003, pp. 643-649.

Bliss, L.C., and Gold, W.G. “Vascular plant reproduction, establishment, and growth and the effects of cryptogamic crusts within a polar desert ecosystem, Devon Island, N.W.T., Canada”. *Canadian Journal of Botany*, Vol. 77, No. 5, 1999, pp. 623-636.

Boeken, B., Ariza, C., Gutterman, Y., and Zaady, E. “Environmental factors affecting dispersal, germination and distribution of *Stipa capensis* in the Negev Desert, Israel”. *Ecological Research*, Vol. 19, 2004, pp. 533-540.

Bowker, M.A., Belnap, J., Rosentreter, R., Graham, B. “Wildfire-resistant biological soil crusts and fire induced loss of soil stability in Palouse prairies, USA”. *Applied Soil Ecology*, Vol. 26, No.1, 2004, pp. 41-52.

Bu, C.F., Wu, S.F., Han, F.P., Yang, Y.S., and Meng, J. “The Combined Effects of Moss-Dominated Biocrusts and Vegetation on Erosion and Soil Moisture and Implications for Disturbance on the Loess Plateau, China”. *Plos One*, Vol. 10, No. 5, 2015.

Castillo-Monroy, A.P., Maestre, F.E., Delgado-Baquerizo, M., Gallardo, A. “Biological soil crusts modulate nitrogen availability in semi-arid ecosystems: insights from a Mediterranean grassland”. *Plant and Soil*, Vol. 333, No. 1-2, 2010, pp. 21-34.

Clément, B.and Touffet, J. “Plant strategies and secondary succession on Brittany Heathlands after severe fire”. *Journal of Vegetation Science*, Vol. 1, No. 2, 1990, pp. 195-202.

Cole, David N. “Trampling disturbance and recovery of cryptogamic soil crusts in Grand Canyon National Park”. *Great Basin Naturalist*, Vol. 50, No. 4, 1990, pp. 321-325.

Deines, Lynell, Rosentreter, Roger, Eldridge, David J. and Serpe, Marcelo D. “Germination and seedling establishment of two annual grasses on lichen-dominated biological soil crusts.” *Plant Soil*, Vol. 295, 2007, pp. 23-35.

Gardner, Charles R., and Mueller, Dale M.J. “Factors Affecting the Toxicity of Several Lichen Acids: Effect of pH and Lichen on Acid Concentration”. *American Journal of Botany*, Vol. 68, No. 1, 1981, pp. 87-95.

Godinez-Alvarez, H., Morin, C., and Rivera-Aguilar, V. “Germination, survival, and growth of three vascular plants on biological soil crusts from a Mexican tropical desert”. *Plant Biology*, Vol. 14, No. 1, 2012, pp. 157-162.

Harper, Kimball T. and Belnap, Jayne. “The influence of biological soil crusts on mineral uptake by associated vascular plants.” *Journal of Arid Environments*, Vol. 47, 2001, pp. 347-357.

Hawkes, Christine V. “Effects of Biological Soil Crusts on Seed Germination of Four Endangered Herbs in a Xeric Florida Shrubland during Drought.” *Plant Ecology*, Vol 170, No. 1, 2004, pp. 121-134.

Jeschke, Michael, and Kiehl, Kathrin. “Effects of a dense moss layer on germination and establishment of vascular plants in newly created calcareous grasslands”. *FLORA*, Vol. 203, No. 7, 2008, pp. 557-566.

Johansen, J.R., 2003. Impacts of fire on biological soil crusts. In: Belnap, J., Lange, O. (Eds.), Biological Soil Crusts: Structure, J. Belnap et al. / Applied Soil Ecology 32 (2006) 63–76 75 Functio

Johansen, J.R., St. Clair, L.L., Webb, B.L., Nebeker, G.T. “Recovery patterns of cryptogamic soil crusts in desert rangelands following fire disturbance”. *The Bryologist*, Vol. 87, No. 3, 1984, pp. 238-243.

Kidron GJ, Aloni I. The contrasting effect of biocrusts on shallow-rooted perennial plants (hemicryptophytes): Increasing mortality (through evaporation) or survival (through runoff). *Ecohydrology*. 2017:e1912. https://doi.org/10.1002/eco.1912

[A] Langhans, Tanja Margrit, Storm, Christian and Schwabe, Angelika. “Biological soil crusts and their microenvironment: Impact on emergence, survival and establishment of seedlings.” *Flora - Morphology, Distribution, Functional Ecology of Plants*, Vol. 204, No. 2, 2009, pp. 157-168.

[B] Langhans, Tanja Margrit, Storm, Christian, and Schwabe, Angelika. “Community Assembly of Biological Soil Crusts of Different Successional Stages in a Temperate Sand Ecosystem, as Assessed by Direct Determination and Enrichment Techniques.” *Microbial Ecology*, Vol. 58, No. 2, 2009, pp. 394-407.

Li, X.R., Jia, X.H., Long, L.Q., and Zerbe, S. “Effects of biological soil crusts on seeds bank, germination and establishment of two annual plant species in the Tengger Desert (N China)”. *Plant and Soil*, Vol. 277, 2005, pp. 375-385.

Liu, Y.M., Xing, Z.S., and Yang, H.Y. “Effect of biological soil crusts on microbial activity in soils of the Tengger Desert (China)”. *Journal of Arid Environments*, Vol. 144, 2017, pp. 201-211.

O’Bryan, Katharine E., Prober, Suzanne Mary, Lunt, Ian D., and Eldridge, David J. “Frequent Fire Promotes Diversity and Cover of Biological Soil Crusts in a Derived Temperate Grassland.” *Oecologia*, Vol. 159, No. 4, 2009, pp. 827-838.

Rice, Steven K., Westerman, B., and Federici, R. “Impacts of the exotic, nitrogen-fixing black locust (*Robinia pseudoacacia*) on nitrogen-cycling in a pine-oak ecosystem”. *Plant Ecology*, Vol. 174, No. 1, 2004, pp. 97-107.

Sedia, Ekaterina G., and Ehrenfeld, Joan G. “Lichens and mosses promote alternate stable plant communities in the New Jersey Pinelands”. *Oikos*, Vol. 100, No. 3, 2003, pp.447-458.

Serpe, Marcelo D., Orm, Jeanne M., Barkes, Tara, and Rosentreter, Roger. “Germination and Seed Water Status of Four Grasses on Moss-Dominated Biological Soil Crusts from Arid Lands.” *Plant Ecology*, Vol. 185, No. 1, 2006, pp. 163-178.

Serpe, Marcelo D., Zimmerman, Shawna J., Deines, Lynell, and Rosentreter, Roger. “Seed water status and root tip characteristics of two annual grasses on lichen-dominated biological soil crusts.” *Plant Soil*, Vol. 303, 2008, pp. 191-205.

Smith, S.M., Abed, R.M.M., and Garcia-Pichel, F. “Biological Soil Crusts of Sand Dunes in Cape Cod National Seashore, Massachusetts, USA”. *Microbial Ecology*, Vol. 48, No. 2, 2004, pp. 200-208.

Song, G., Li, X., and Hui, R. “Effect of biological soil crusts on seed germination and growth of an exotic and two native plant species in an arid ecosystem”. *Plos One*, Vol. 12, No. 10, 2017.

Su, Yan-gui, Li, Xinrong, Zheng, J. and Gang, Huang. “The effect of biological soil crusts of different successional stages and conditions on the germination of seeds of three desert plants.” *Journal of Arid Environments*, Vol. 73, No. 10, 2009, pp. 931-936.

Thiet, Rachel K., Doshas, Alexis, Smith, Stephen M. “Effects of biocrusts and lichen-moss mats on productivity in a US sand dune ecosystem” *Plant and Soil*, Vol. 377, No. 1-2, 2014, pp. 235-244.

Zaady, Eli, Gutterman, Yitzchak and Boeken, Bertrand. “The germination of mucilaginous seeds of *Plantago coronopus*, *Reboudia pinnata*, and *Carrichtera annua* on cyanobacterial soil crust from the Negev

Desert.” *Plant and Soil*, Vol. 190, No. 2, 1997, pp. 247-252.

Zhang, Y.M., Aradóttir, A., Serpe, M., and Boeken, B. “Interactions of biological soil crusts with vascular plants”. *Biological Soil Crusts: An Organizing Principle in Drylands* (eds.) Weber, B., Büdel, B., and Belnap, J. Ecological Studies Series 226, Berlin, Germany, Springer-Verlag, 2016, pp. 385-406.

Figures and Legends

Table 2) ANOVA table of the relationship of germination with soil type, plant species, and their interaction. Respective P-values are shown for the three categories.

Variable	**DF**	**F**	**P-Value**
Soil Type	**1**	**54.4**	**0.0001**
Plant Species	1	0.2	0.6
Soil Type * Plant Species	1	2.4	0.13
Residuals	36	-	-

Figure 1) A box-and-whisker plot showing the total number of seeds germinated (out of 20) on and off crust for both bush clover and lupine.

Figure 2) A plot of the cumulative number of germinated seeds for bush clover and lupine on bare soil and crust conditions over the span of 35 days.